BIOTROPIA NO. 24, 2005 : 30 - 45

ANALYSIS OF THE TEMPERATURE DEPENDENCE OF CO_2 ASSIMILATION RATE (STUDY CASE: *GLYCINE MAXL.* MERR)

TANIA JUNE

BIOTROP-JCSEA, SEAMEO BIOTROP, BTIC Building,
Jl. Raya Tajur Km. 6 Bogor, Indonesia; email: taniajune@biotrop.org;
Laboratory o/Agrometeorology, Bogor Agricultural University, Bogor

ABSTRACT

The maximum rate of carboxylation (K_{cmax}) and maximum rate of regeneration of *Ribulose bisphosphate* (RuBP) (controlled by the rate of electron transport, J_{max}) arc two processes governing the photosynthetic capacity of plants. Both processes are affected by temperature. This paper examines how the response of these two photosynthetic capacities to temperature determines the temperature response curve of the CO_2-assimilation rate for plants grown at different temperatures, by using the concept of the *Farquhar €3* photosynthesis model. The goal is to use photosynthetic parameters from CO_2 and light curves to predict the temperature dependence of the CO_2-assimilation rate *(A)* of soybean and to estimate the preferred growth temperature. Analysis shows that the optimum temperature of the assimilation rate changes with the changing temperature dependence of carboxylation and regeneration of RuBP.

Key words : temperature dependence/soybean/modeling photosynthesis/preferred growth temperature.

INTRODUCTION

Photosynthesis is strongly affected by temperature. During gas exchange measurements, the short-term temperature dependence of photosynthesis is strongly affected by other environmental factors such as light intensity and intercellular COa concentration (Berry & Bjorkman 1980). Some of these short-term effects can be modeled by C_3 photosynthesis models of Farquhar *et al.* (1980). However, the response varies not only among species but even within an individual species subjected to changing growth temperature regimes during their developments (long-term effects) (Berry & Bjorkman 1980). In many species, the optimum temperature at which maximum short-term photosynthesis is obtained, shifts upwards when plants are grown at higher temperatures (Lange *et al.* 1974; Slatyer 1977; Berry & Bjorkman 1980; Ferrar, Slatyer & Vranjic 1989), which is commonly known as acclimation or adaptation. The long-term temperature acclimation during growth may affect both the maximum photosynthetic rate per unit leaf area and the shape of the photosynthetic temperature response curve. How this growth temperature (long-term effect) affects the short-term temperature response of photosynthesis is still unclear. It can be attributed at the enzyme level or at the gene action-DNA level. To understand the mechanism of this change in temperature dependence, it is important to know the limiting factor to photosynthesis at each measured temperature.

According to the Farquhar *Cj* photosynthesis model (Farquhar *et al.* 1980), carboxylation and regeneration of RuBP are two processes governing photosynthesis. In the model, the photosynthetic rate is limited either by the capacity of RuBP carboxylase (Rubisco) to consume ribulose bisphosphate (RuBP), denoted as F_{cmax}, or by the capacity for RuBP regeneration, denoted as $J_{ma}x/4$. These capacities have different temperature dependencies, in the original model and as confirmed, for example, by Kirschbaum & Farquhar (1984) and later by June (2002).

For a fixed temperature dependence of the electron transport rate *(J),* Farquhar & von Caemmerer (1982) showed that increasing the ratio of the capacity of Rubisco to consume RuBP to that of RuBP regeneration could change the optimum temperature (r_o) by changing the relative amounts of the two components, so that the optimum temperature would be higher when the ratio is increased. June (2002) has shown that this ratio decreased with increasing temperature. However, June (2002) also showed that temperature dependence of electron transport rate is not fixed but changed, both at short-term and long-term time scales. The net effect is on the change in the ratio J_{mm}/V_{cmm} with temperature. In the Farquhar & von Caemmerer (1982) paper, the ratio of RuBP consumption to RuBP regeneration increased with increasing growth temperature. In June (2002), the *Jmm/Vcmax* ratio decreased as the short-term temperature measurement increased, for each of the growth condition.

This paper examines how the changes in these two photosynthetic capacities with temperature affect the temperature response curve of the CO2-assimilation rate for plants grown at different temperatures, using the concept of the Farquhar *et al.* (1980) C_3 photosynthesis model. The goal is to use parameters from CC>2 and light curves from June (2002) *(V_{cmm}* and J_{max} temperature dependences) to predict the temperature dependence of the CO_2-assimilation rate *(A)* and then to test the model with independent measurements of the temperature dependence of the CC>2-assimilation rate. The plants used for testing the model were grown under the same conditions as the plants used for the parametrisation of the model in June (2002).

MATERIALS AND METHODS

Seeds of indeterminate soybean *(Glyclne max* [L.] Merr. cv Stephen) were sown in 12 liter plastic pots containing a mixture of sand and vermiculite (1:1, v/v) and plants were thinned to one plant per pot after germination. Plants were grown in a controlled environment chamber with a 14-hour photoperiod of around 700 umol quanta m"^{2} s"', 60/70 % relative humidity day/night and three different temperature regimes: 20/15, 25/20, 32/27 day/night °C under ambient [CO_2], 350 umol mol'^{1}. The lowest and highest temperature regimes were repeated with atmospheric [CCy enrichment to 700 umol mol"^{1}.

The source of light used in the growth chamber was a metalarc lamp (General Electric Lighting), MVR 1000/U. Plants were well spaced (30 cm apart at sowing) to avoid mutual shading. Rhizobial inoculation was not provided for the plants. Each

pot was flushed every second day with full-strength Herridge's solution (0.50 mM $MgSO_4$, 0.25 mM $CaCl_2$, 0.25 mM KC1, 0.125 mM KH_2PO_4, 0.125 mM K_2HPO_4, 25 uM ferric monosodium salt of EDTA, 12 uM H_3BO_3, 3.6 uM $MnCl_2$, 77 uM $ZnCl_2$, 76 nM $CuCl_2$, 25 nM $NaMoO_4$) (Herridge 1977) and watered twice daily on days when nutrients were not given. To obtain a range of nitrogen levels in the plant leaves, three different concentrations of KNO_3 were added to the nutrient solution (2, 5 and 16 mM). The nutrient solutions were added to each pot until they drained at the base (2.5 to 3.0 liters per pot).

For gas exchange measurement, several temperature response curves of assimilation rate were measured at a light intensity of 1200 umol m~^{2} s"^{1} with CO_2 concentrations of 350 umol mol"^{1} using a photosynthetic gas exchange system developed in the Environmental Biology Group, Research School of Biological Sciences, Australian National University. Two pots of plants were used for replication. The vapour pressure difference was kept constant at around 12.5 mbar in most cases and was less than 17 mbar in all cases. For each leaf, the CO_2-assimilation rate was measured at six temperatures from 15°C to 40°C, holding for 15 to 20 minutes at each temperature measurement to reach a steady state condition. Data obtained from measurements are then compared to simulation results where parameters are obtained from measurements by June (2002).

RESULTS AND DISCUSSION

Temperature dependence of CO_2 assimilation rate

Figure 1 shows the temperature dependence of the absolute value of the CO_2-assimilation rate *(A)* measured at 350 umol mol"^{1} [CO_2] and irradiance of 1200 umol m"^{2} s"^{1}, for plants grown under 350 umol mol^1 [CO_2]. As expected, increasing the temperature from 15°C to 25°C increases the assimilation rate: 18 % for plants grown at 20/15°C (day/night temperature), 88 % for plants grown at 25/20°C and 98 % for plants grown at 32/27°C. Increasing the measurement temperature further resulted in *A* reaching a maximum at the optimum temperature and then decreasing. After reaching the optimum temperature, the photosynthesis rate dropped with further increasing temperature; by 40°C the drop in *A* was as much as 10 % for plants grown at 20/15°C, 24 % for plants grown at 25/20°C and 10 % for plants grown at 32/27°C. It is clear that the temperature dependence of the CO_2-assimilation rate is different depending on the growth temperature.

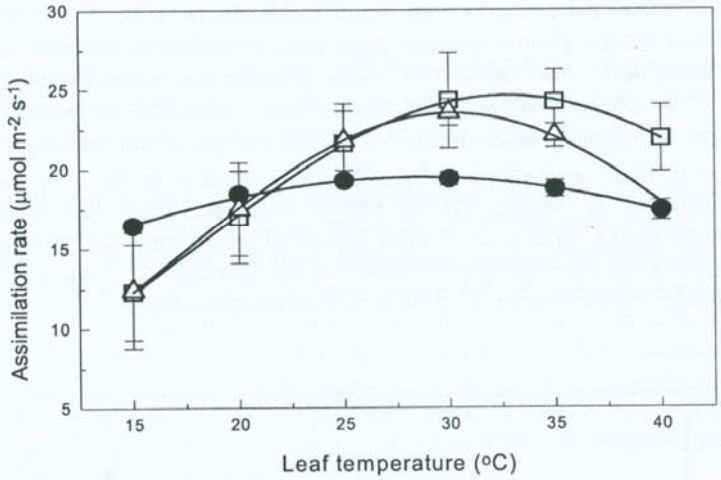

Figure 1. Temperature dependence of the CO_2-assimilation rate of soybean grown at day/night temperatures of 20/15 °C (●), 25/20 °C (Δ) and 32/27 °C (□). Plants were grown at a [CO_2] of 350 µmol mol^{-1} and measured at the same concentration. Irradiance was 1200 µmol m^{-2} s^{-1}. Optimum temperature (T_o) and assimilation rate at optimum temperature A (T_o) are given in Table 1. Solid lines are fitted to Eq. (7). Error bars are standard error.

The photosynthetic processes in soybean exhibit a capacity for temperature acclimation. Plants maintained at different day/night temperatures had different optimum photosynthetic temperatures *(T_0)*. Plants grown at 32/27°C have an optimum temperature for the CO_2-assimilation rate of 32.7±0.2°C. When plants were grown at 25/20°C, the optimum temperature was 30.1±0.8°C and when plants were grown at 20/15°C, the optimum temperature was reduced to 28.5 ±0.9°C (Table 1).

Table 1. Optimum temperature for COz assimilation rate, 7"$_0$, and assimilation rates, *A,* at optimum temperature and at various other temperatures for plants growing at different temperatures,+ s.c. Plants were grown at the temperatures indicated in the table, CO_2 concentration of 350 (imol mol"^{1} and nitrogen concentration of 16 mM. Gas exchange measurements were conducted at [CO_2]=350 (imol mol"' and light intensity, 7=1200 ^mol m"^{2} s"'.

Growth temperature	20/15 °C	25/20 °C	32/27 °C
T_o	28.5 ± 0.9	30.1 ± 0.8	32.7 ± 0.2
A (at T_o)	18.9 ± 0.3	22.8 ± 0.8	24.6 ± 2.0
A (at 20 °C)	17.9 ± 0.2	17.0 ± 2.8	17.0 ± 2.9
A (at 25 °C)	18.7 ± 0.3	21.1 ± 1.8	21.6 ± 2.5
A (at 35 °C)	18.2 ± 0.5	21.4 ± 0.7	24.4 ± 2.0

In a similar study with *Festuca arundinaceae* grown at 10 and 25°C, Treharne & Nelson (1975) found that at measurement temperatures above 15°C, net photosynthesis rates per unit area were higher in plants grown at 25°C. The authors concluded that greater photorespiration rates were important in accounting for the low net photosynthetic rates of the 10°C plants at higher temperature measurements. However, in the photosynthesis model used in this manuscript, photorespiration is already taken into account in the form of F * (CO_2 compensation partial pressure in the absence of dark respiration) and *c*\ (CO_2 concentration in the intercellular air spaces). Treharne & Nelson (1975) further concluded that the decrease in photosynthesis above 30°C seen in both groups of plants was due primarily to a decrease in stomatal conductance, and hence *c*\, the decrease in *c*\ was not observed in my results (as seen in Figure. 2) with increasing temperature.

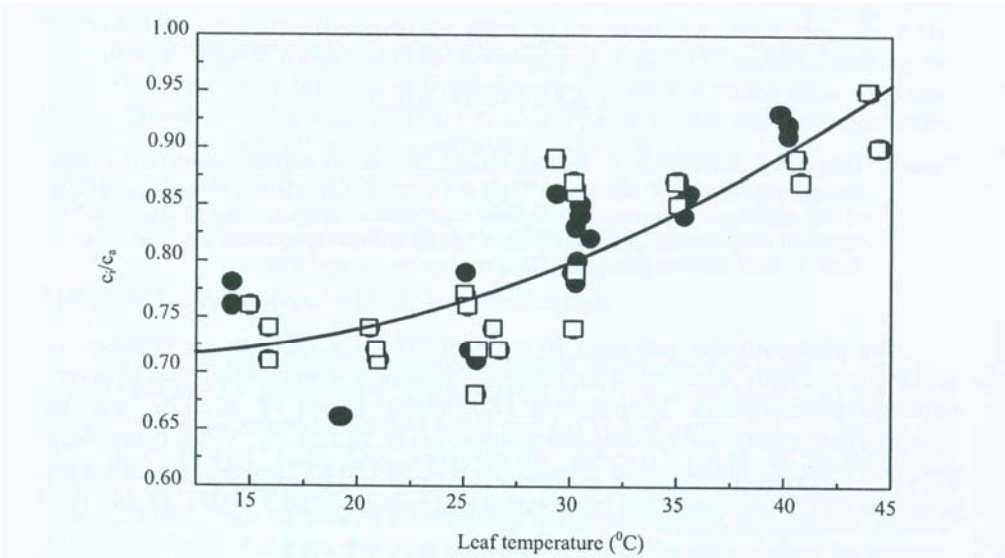

Figure 2. The effect of measurement temperature on the ratio c_i/c_a of plants grown at 20/15°C (●)and 32/27 °C (□) and $[CO_2]$ = 700 µmol mol^{-1}. The solid line is a fitted second degree polynomial $y = 0.76 + 0.00587\ (T\text{-}25) + 1.68x10^{-4}\ (T\text{-}25)^2$ (with $R^2 = 0.73$, N = 53, $P < 0.0001$).

for net CC>2 uptake for plants grown at day/night temperature of 10/10°C was 12°C for *Agave americana* and 15°C for *A. deserti.* When the growth temperature was raised to 30/30°C, the optimum temperature shifted upward by 7°C for *A. americana* and 3°C for *A. deserti.* Shifting *A. americana* to the higher growth temperature caused the maximum rate of net CC>2

uptake at the optimal temperature to increase, whereas the same shifting of *A. deserti* caused it to decrease. The results showed that $A(T_0)$, *i.e.* the optimum temperature for net assimilation rate or rate of photosynthesis, increase with increasing growth temperature.

Plants grown under 700 ^mol mol"' [CO_2] exhibited a similar pattern as those grown under ambient [CO_2], with T_0 = 28.0 ± 0.4 and 32.2 + 0.7°C and $A(T_0)$ = 20.7 + 2.0 and 21.8 ± 0.7 tamol $m^{'2}$ s^{ij} for plants grown at 20/15 and 32/27°C, respectively.

It is important to note that a change in *c* (the intercellular CC>2 concentration) can cause a shift in the optimum temperature of photosynthesis, with T_0 increasing with *Ci* (Farquhar & von Caemmerer 1982; Kirschbaum & Farquhar 1984).

There is a linear correlation between growth temperature and the optimum temperature for CO_2 assimilation rate (Figure 3). The linear regression from Table 1 can be solved to give a "preferred" temperature for the CC>2 assimilation rate of 33°C. This concept of "preferred" temperature was initially suggested by Slatyer & Ferrar (1977), and is the intersection of the linear regression line and the 45° line. The "preferred temperature" was also used in June (2002) to descibe the acclimation of the electron transport rate *(J)* to growth temperature.

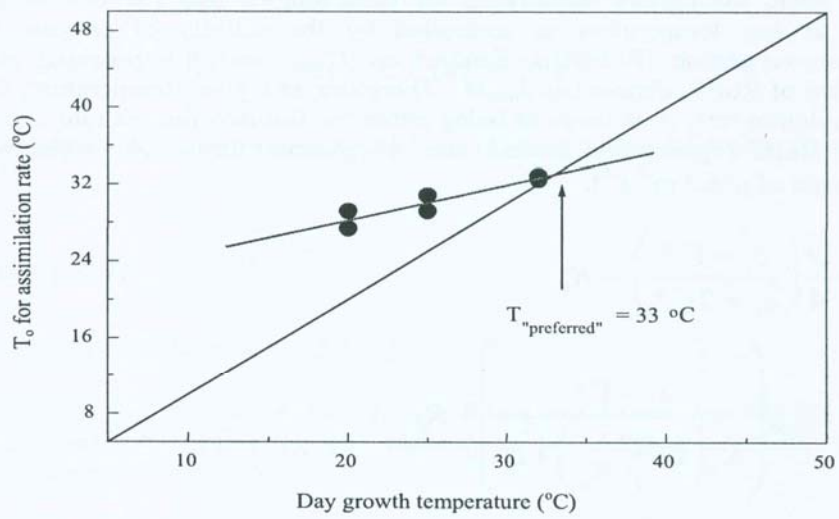

Figure 3. Relationship between the measured optimum temperature for CO_2 assimilation rate and the day growth temperature. The intersection of the regression line with the 1:1 line gives the "preferred" growth temperature of 33°C for the CO_2-assimilation rate. The regression equation between the day growth temperature (T) and optimum temperature for assimilation rate (T_o) is $T_o = 20.4 + 0.38\ T$ with $R^2 = 0.9$. Values were obtained using Eq. (7).

What controls the reduction in CO_2assimilation rate after reaching optimum temperature?

It has been reported that high temperature limits CO_2 availability, because c the physiological responses of leaves which result in increased resistance to the ga diffusion (Mukohata *et al.* 1971; Monson *et al.* 1982). High temperature also alter the substrate specificity of Rubisco (Jordan & Ogren 1984; Brooks & Farquha 1985) and its activity (Weis 1981; Santarius *et al.* 1991). Working with *Neriun oleander,* Badger *et al.* (1982) showed that plants grown at low temperature ha< higher activity of several photosynthetic enzymes at low temperatures but had lowe heat stability relative to plants grown at high temperatures. Temperature acclimatioi in the electron transport system could also be the reason for the change in the CO: assimilation rate at high temperature. Several studies have shown that the temperature dependence of electron transport capacity changes with growtr temperature (Armond *et al.* 1978; Badger *et al.* 1982; Mitchell & Barber 1986) Such changes were also observed in June (2002), where plants grown at highei temperature had a lower electron transport rate.

Modeling the temperature dependence of the CO_2-assiinilation rate

The basic assumption underlying the modelling is that the rate of photosynthesis at any temperature is controlled by the activity of enzyme RuBP carboxylase-oxygenase (Rubisco), denoted as V_{cmm}, and the potential rate of regeneration of RuBP, denoted as $J_{max}/4$. Therefore, at a given temperature, the net CO_2-assimilation rate, *A,* is taken as being either the Rubisco-limited rate, A_v, or the estimated RuBP-regeneration-limited rate of photosynthesis, *Aj,* whichever is smaller (units of umol m^{-2} s^{-1}).

$$A_j = \frac{J}{4}\left(\frac{c_i - \Gamma *}{c_i + 2\Gamma *}\right) - R_d \qquad (1)$$

$$A_v = V_{c\max}\left(\frac{c_i - \Gamma *}{K_c\left(1 + O/K_o\right) + c_i}\right) - R_d \qquad (2)$$

where *c*\ = partial pressure of CO_2 in the leaf, F* = CO_2 compensation partial pressure in the absence of dark respiration, /?$_d$ = dark respiration by the leaf which continues in the light, *O* = ambient partial pressure of oxygen, and AT_C and K_0 are the Michaelis-Menten constants for carboxylation and oxygenation by Rubisco, respectively. Temperature dependence of *c*\ follows the equations from Figure 2. *R^* follows this equation:

$$R_d = A_1 + A_2(T\text{-}25) + A,(T\text{-}25)^2 \quad (3)$$

where Tis leaf temperature (°C) and ,4], $A_2 and Ai$ are the fitted parameters of the R_f temperature relationship (Table 2), which was obtained from June (2002). The temperature dependence of K_c and K_0 follows an Arrhenius function as

$$K_c = K_{c,25} \exp\left[\frac{E_c}{298.2R}\left(1 - \frac{298.2}{(T + 273.2)}\right)\right] \quad (4)$$

$$K_o = K_{o,25} \exp\left[\frac{E_o}{298.2R}\left(1 - \frac{298.2}{(T + 273.2)}\right)\right] \quad (5)$$

where R is the Universal gas constant, 8.3144 J mol"[1] K"'. E_f and E_0 are the apparent activation energies with the 25 subscript representing the value at 25°C.

The effect of temperature on the CC>2 compensation point of photosynthesis in the absence of mitochondrial (dark) respiration follows the equation of von Caemmerer *et al.* (1994), assuming infinite wall conductance.

$$\Gamma^* = 36.9 + 1.88(T - 25) + 0.036(T - 25)^2 \quad (6)$$

The temperature dependence *ofJ* and F_{cmax} is given by the following equations June (2002):

$$J(T) = J(T_o)e^{-\left(\frac{T-T_o}{\Omega}\right)} \quad (7)$$

$$V_{cmax} = C_1\,[1 + C_2(T\text{-}25) + C_3(T\text{-}25)^2], \quad (8)$$

where J(T_0), T_0, Q, $C\backslash$, C_2 and C_3 are the fitting parameters, specific for each set of growth conditions (Table 2). The capacity of the electron transport rate can be inferred from

$$J_{max} = \frac{I_2 J - \Theta J^2}{I_2 - J} \quad (9)$$

where the light dependence of electron transport, J, follows the equation by .Farquhar & Wong (1984):

$$J = \frac{Ia_2 + J_{max} - \sqrt{(Ia_2 + J_{max})^2 - 4\Theta Ia_2 J_{max}}}{2\Theta} \quad (10)$$

•/max is the maximum (light-saturated) rate of electron transport capacity of the leaf, 0 is the curvature factor of the light response curve of Eq. (10) and *a-i* is the quantum yield of electron transport. / is the amount of light intensity incident on the leaf surface. /2 in Eq. (9) is equal to *021.* The temperature dependence of © follows the equation of June (2002):

$$\Theta = T_1 + T_2(T - 25) + T_3(T - 25)^2 \quad (11)$$

where *T*\= 0.93, T_2 = 0.0145, and *T*-> = -8.13 the $W^{4'}$ These curvature factor parameters were obtained from June (2002), where measurement of the light curves was done with light incident on both the upper and lower surface of the leaf.

Table 2. Photosynthesis parameters used in the simulation based on parameterization done on soybean (June 2002).

Parameter	Growth temperature (°C)			Activation energy
	20/15	25/20	32/27	
$K_{c,25}$ (Pa)		40.4*		59400**
$K_{o,25}$ (Pa)		24800*		36000**
T_1 (for Θ)		0.93		
T_2 (for Θ)		0.0145		
T_3 (for Θ)		-8.13×10^{-4}		
Ω	17.0	17.6	19.2	
$J(T_o)$	243.3	215.7	183.6	
A_1 (for R_d)		0.328		
A_2 (for R_d)		-0.051		
A_3 (for R_d)		0.00299		
C_1 (for V_{cmax})	110.53	111.14	99.35	
C_2 (for V_{cmax})	0.083	0.061	0.066	
C_3 (for V_{cmax})	2.4×10^{-3}	9.9×10^{-4}	5.0×10^{-4}	
a_2		0.3		
T_o for J (°C)	35.5	37.8	38.8	
Γ* (Pa)		3.69*		

*von Caemmerer *et al.* (1994); **Badger and Collatz (1977). The values for all parameters were taken from June (2002), representing plants grown at 20/15, 25/20 and 32/27 °C and [CO_2] of 350 µmol mol^{-1}. Parameters which have only one number are an average of all growth conditions.

Simulated CO_2 assimilation rate

The simulation results, based on Table 2, at measurement temperatures of 15 to 40°C and / = 1200 umol m"^{2} s"^{1}, are shown in Figure 4. Figure 5 shows the results for $J_m$ax, converted from *J* using Eqs. (9) to (11). F_{cmax} is constantly increasing with temperature, in relatively good agreement with Wang *et al.* (1996) and other estimates (Wullschleger 1993). However, Ferrar *et al.* (1989) who investigated several species of *Eucalyptus* grown at contrasting temperatures found that in leaves grown at high temperature, F"$_{cmax}$ increased with short-term temperature measurement, but in leaves grown at low temperature, K_{cmax} did not increase as measurement temperature increased. They speculated that Rubisco may be inactivated or damaged at measurement temperatures higher than the growth temperature. In my experiment, although F_{cmax} increases with short-term temperature measurements for all growth conditions, plants grown at higher temperature have a slightly lower Fc_{max} than plants grown at lower temperature.

June (2002) showed that there is an acclimation in the electron transport rate which favours the lower growth temperature (20/15 °C). Hence, if there is no stomatal effect due to different growth temperatures, then the CO_2-assimilation rate of plants grown at 20/15 °C will be higher than that of plants grown at 32/27 °C in the model (as seen in Figure 4).

The lower observed CO_2-assimilation rate of plants grown at 20/15°C (Figure 1), and their lower assimilation rate at T_0, make these plants a poor representation of this simulation (compare Figure 1 and Figure 4). The standard measurements of those particular leaves (standard measurement was done at light intensity of 1200 umol irfV, vpd =12.5 mbar, [CCy = 350 umol mol"', and temperature = 25°C), before starting each measurement were lower on the first day the plants were taken out from the growth chamber (the day when those measurements were done). They were increased by 19.5 % the next day. If the data (of the 20/15°C plants) were corrected with this percentage, plus taking into account the reduced $c_{i(}$ then the CO_2-assimilation rate at T_0 of plants grown at 20/15°C would be higher than the other two growth temperature of plants as shown by the simulation result in Figure 4.

The simulation shows that differences in the temperature dependence of *A* are due to the differences in the processes limiting^. For example, *A* for 20/15 °C plants is limited by RuBP regeneration below 23°C and is limited by Rubisco activity at temperatures higher than 23°C, while A for 32/27°C plants is limited by RuBP regeneration below 30°C and is limited by Rubisco activity at temperature higher than 30°C. For plants grown at 25/20°C, *A* was limited by RuBP regeneration below 28°C and limited by Rubisco activity at temperature higher than 28°C. A co-limitation of these two capacities occurs at the optimum temperature (where A_v and *AJ* lines cross in Figure 4) and only one of them would limit photosynthetic rate at other temperatures, with the penalty of excess investment in the other capacity. Therefore, when growth temperatures vary, changes in the organization of the photosynthetic apparatus are necessary, and this can be shown by the changed optimal ratio of Jmaxs / Vmaxs (Farquhar & Caemmerer 1982).

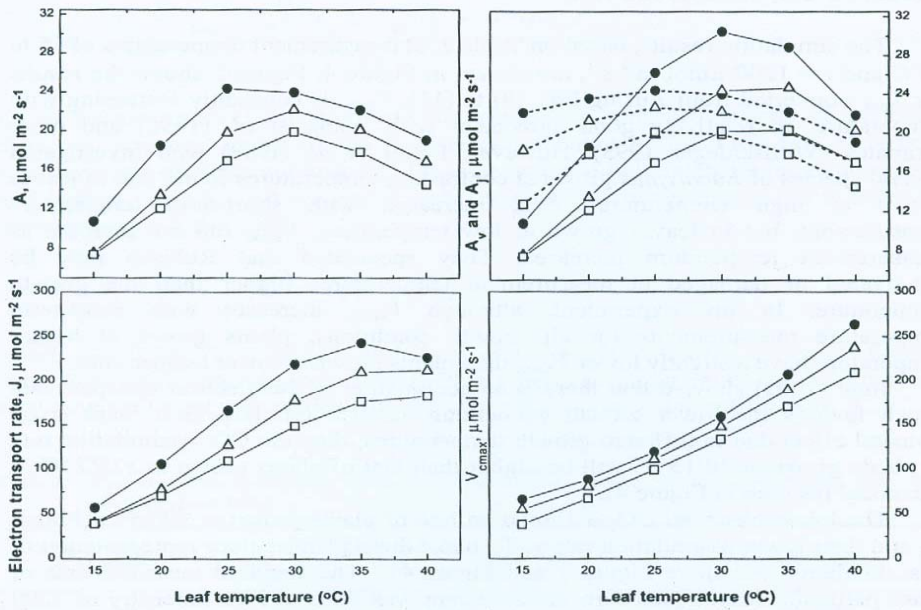

Figure 4. Simulated temperature dependence of the CO_2-assimilation rate (A), assimilation rate limited by RuBP regeneration (A_j) (solid line) and limited by Rubisco (A_v) (dashed line), electron transport rate (J) and maximum rate of Rubisco activity (V_{cmax}). Different symbols indicate plants grown at different temperatures: 20/15 °C (●), 25/20 °C (Δ) and 32/27 °C (□). Simulation was done at irradiance of 1200 µmol m^{-2} s^{-1}. c_i was kept constant across growth temperatures and measurement temperatures at 0.7 c_a, assuming wall conductance $g_w = \infty$.

The simulated ratio of Jmaxs / Vcmaxs

Figures 4 and 5 show that between 15 and 35°C, the relative slope of the increase in J_{max} is higher than it is in F_{cmax}; then the opposite happens with further increase in temperature. As the slope of increase in J_{max} with temperature was higher than that of F_{cmax} within the range of 15 - 30°C (Figures 4 and 5), the simulation predicts that the ratio of J_{max}/V_{cmax} would increase with temperature within this range. Figure 5 indicates that plants change the allocation of their photosynthetic resources between these two capacities as growth temperature changes. June (2002) showed that ./$_{max}$/F_{cmax} did have a lower value when plants were grown at 32/27°C compared to plants grown at lower temperatures, which is supported here by the simulation.

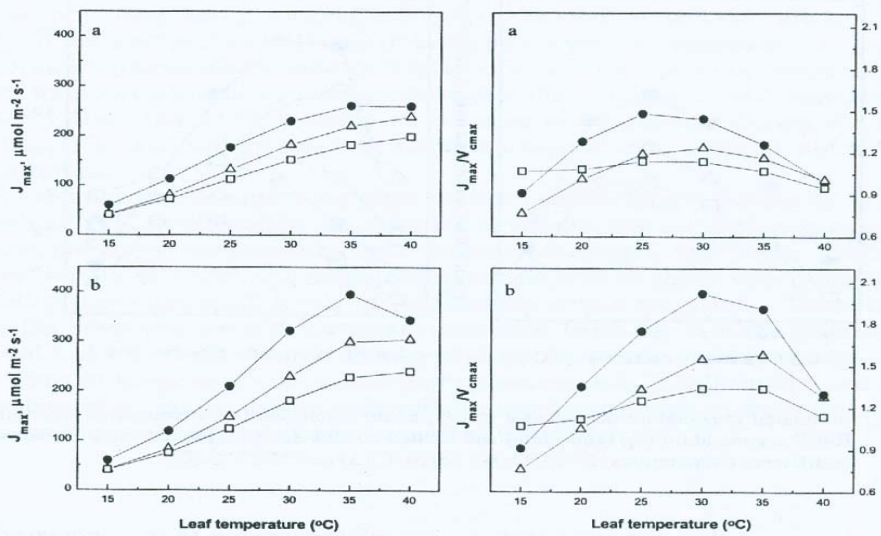

Figure 5. Simulated temperature dependence of light saturated electron transport capacity (J_{max}) and the ratio of J_{max}/V_{cmax} with (a) Θ changing with temperature as in Eq. (11) and (b) Θ constant at 0.7. Different symbols indicate simulations for plants grown at different temperatures: 20/15°C (●), 25/20 °C (△) and 32/27 °C (□).

Farquhar & *von* Caemmerer (1982) and recently Hikosaka (1997) predicted that the photosynthetic rate should be co-limited by F_{cmax} and J_{max} at the growth temperature for efficient nitrogen utilization of photosynthesis. Figure 4 shows that the temperature where the two processes co-limit photosynthesis in the simulation (i.e. where A_v and *Aj* lines cross) was close to the growth temperature. It was around 23°C for plants grown at 20/15°C, 27 °C for plants grown at 25/20°C and 30°C for plants grown at 32/27°C. The slight differences are probably due to the different light intensity used in the measurement (1200 iimol m"^{2} s'") compared to that in the growth chamber (600-700 umol m~^{2} s'"). Under lower light, the electron transport rate would be lower and it might co-limit at a lower temperature than the ones from Figure 4, which would *improve* the agreement for plants grown at the lower two growth temperatures.

When *J* is converted to J_{max} using Eq. (9), the value depends on which 0 value is used (as shown in Figure 5). Using 0 = 0.7, the estimated J_{max} was higher as tem-

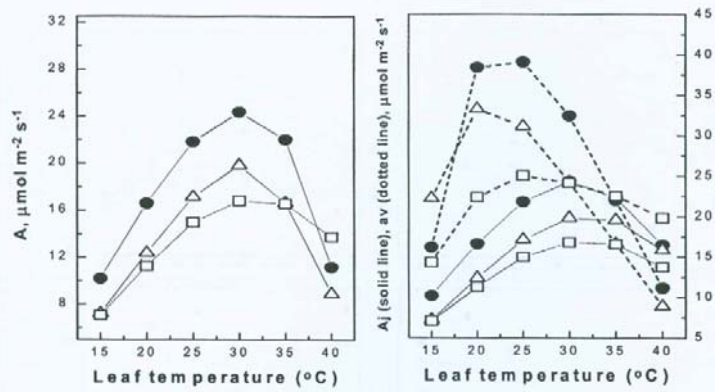

Figure 6. Simulated temperature dependence of CO_2-assimilation rate (A), assimilation rate limited by RuBP regeneration (A_j) (solid line) and limited by Rubisco (A_v) (dotted line) of plants grown at different temperatures: 20/15 °C (●), 25/20 °C (Δ) and 32/27 °C (□).

perature increased than the estimated J_{mn} calculated using a Θ that increased with temperature. This difference affects the ratio of J_{mn}/y_{cmn}, with a higher ratio obtained when Θ was held constant at 0.7.

Now, the temperature where co-limitation occurs changes from that in Figure 4. For plants grown at 20/15 and at 25/20°C, it is almost the same at 33 -35°C. Plants grown at 32/27°C, were always limited by A-$_v$ Figure 6 also shows that for conditions in which electron transport becomes limiting (that is, growth at high temperature), the electron transport rate will dominate the behaviour of the CO_2-assimilation rate, so the optimum temperature of A should shift towards the optimum temperature of J_{mn}.

CONCLUSIONS

The temperature response characteristics of the photosynthetic process are not fixed but depend on the prevailing conditions during growth. The present study shows how the temperature dependence of the photosynthetic rate differs between plants grown at different temperatures. The factors responsible for the difference include the change in temperature dependences of the two processes controlling photosynthesis, carboxylation and regeneration of RuBP. The change in the proportion of photosynthetic resources into these two capacities can be shown by the change of the J_{max}/ V_{cmaxs} ratio with growth temperature.

Acclimation to growth temperature occurred as shown by the changing optimum temperature with growth temperature. This acclimation is important for plants in optimising their photosynthesis rate in the environment they are exposed to in terms of the most economical way of using photosynthetic resources.

For the soybean plants used in this experiment, the optimum temperature for electron transport *(J)* was a few degrees higher than the preferred temperature for CO_2-assimilation rate (33°C). Hence an increase in temperature during the day to more than 33°C will still increase the electron transport rate, although not the CO_2-assimilation rate.

For the purpose of modelling plant growth or modelling the capacity of plants in absorbing CO_2 in relation to the changing environmental conditions (atmospheric CO_2 concentration, temperature, light intensity, nitrogen, and water availability effect on supply of CO_2), the most useful models will be those which incorporate acclimation processes at all levels of organization within the plants. These models will be the most precise and the most responsive to changes in the physical and biological factors which control photosynthesis. However, the knowledge of the mechanisms of temperature dependence of photosynthesis is still limited and so the combination of an empirical approach with the mechanical ones in these areas where the mechanism is already established would be beneficial.

REFERENCES

Armond P. A., Schreibcr U. and O. Bjorkman. 1978. Photosynthetic acclimation to tempe-rature in the desert shrub, *Larrea diraricata.* II. Light Harvesting Efficiency and electron transport. Plant Physiology, 61:411-415.

Badger, M. R. and G.J. Collate. 1977. Studies on the kinetic mechanism of ribulose-l,5-bisphosphate carboxylase and oxygcnase reactions, with particular reference to the effect of temperature on kinetic parameters. Carnegie Institute of Washington Yearbook, 76:355-361.

Badger, M.R., Bjorkman, O. and P.A. Armond. 1982. An analysis of photosynthetic response and adaptation to temperature in higher plants: temperature acclimation in the desert evergreen *Nerium oleander* L. Plant, Cell and Environment, 5: 85-99.

Berry, J. and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. Annual Review of Plant Physiology, 31:491 -543.

Brooks, A. and G.D. Farquhar 1985. Effect of temperature on the $COrO_2$ specificity of ribulose-1,5-bisphosphatc carboxylasc/oxygenasc and the rate of respiration in the light. Estimates from gas exchange measurements on spinach. Planta, 165: 397-406.

Farquhar, G. D. and S. von Caemmerer. 1982. Modelling of photosynthetic responses to environmental conditions. Physiological plant ecology. II. Encyclopedia of Plant Physiology, New Series. O. L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Berlin, Springer-Vcrlag.

Farquhar, G.D., von Caemmerer, S. And J.A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta, 149: 78-90.

Ferrar, P.J., Slatyer, R.O. and J.A. Vranjic. 1989. Photosynthetic temperature acclimation in Eucalyptus species from diverse habitats and a comparison with *Nerium oleander.* Australian Journal of Plant Physiology, 16: 199-217.

Herridge, D.F. 1977. Carbon and nitrogen nutrition of two annual legumes. University of Western Australia. Perth.

Hikosaka, K. 1997. Modelling optimal temperature acclimation of the photosynthetic apparatus in C_3 plants with respect to nitrogen use. Annals of Botany, 80: 721 -730.

Jordan, D. B. and W. L.Ogren 1984. The CO_2/O_2 specificity of ribulose, 1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulosebisphosphate concentration, pH and temperature. Planta, 161:308-313.

June, T. 2002. Environmental Effects on photosynthesis of C3 plants: scaling up from electron transport to the canopy (Study case: *Glycine max* L. Merr). Environmental Biology, Research School of Biological Sciences. Australian National University. Canberra.

Kirschbaum, M.U.F. and G.D. Farquhar. 1984. Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb. ex Spreng. Australian Journal of Plant Physiology, 11: 519-538.

Lange, O.L., Schulze, E.D., Evenari, M., Kappen, L., and U. Buschbom. 1974. The temperature-related photosynthetic capacity of plants under desert conditions. I. Seasonal changes of the photosynthetic response to temperature. Oecologia, 17: 97-110.

Mitchell, R.A.C. and J. Barber. 1986. Adaptation of photosynthetic electron-transport rate to growth temperature in pea. Planta, 169: 429-436.

Monson, R.K., Stidham, M.A., Williams, G.J. and G.E. Edwards. 1982. Temperature dependence of phothosynthesis in *Agropyron smithii* Rydb. Plant Physiology, 69: 921-928.

Mukohata, Y., Mitsudo, M., Kakumoto, S., and M. Higashida. 1971. Biophysical studies on subcellular particles. V. Effects of temperature on the fcrricyanide-Hill reaction, the light-induced pH shift and the light scattering response of isolated spinach chloroplasts. Plant Cell Physiology, 12: 869-80.

Nobel, P.A and T.L. Hartsock. 1981. Shifts in the optimal temperature for nocturnal CO_2 uptake caused by changes in growth temperature for cacti and agaves. Physiologia Plantarum, 53: 523-527.

Santarius, K.A., Exner, M. and R. Thebud-Lassak. 1991. Effect of high temperature on the photosynthetic apparatus in isolated mesophyll protoplasts of *VaUrianella locusta* (L.) Betcke. Photosynthetica, 25: 17-26.

Slatyer, R.O. 1977. Altitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. Ex Spreng. IV. Temperature response of four populations grown at different temperatures. *Australian Journal of Plant Physiology,* 4: 595-609.

Slatyer, R.O. and P.J. Ferrar. 1977. Altitudinal Variations in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. Ex Spreng. V. Rate of acclimation to an altered growth environment. Australian Journal of Plant Physiology, 4: 595-609.

Trehame & Nelson 1975 *In:* Plants and Temperature. (*Eds.* S.P. Long and F.I. Woodward). Symposium of the Society of Experimental Biologists, vol. 42. Cambridge: Company of Biologists, p. 329-346.

von Caemmerer, S., Evans, J.R., Hudson, G.S. and T.J. Andrews. 1994. The kinetics of Rubisco inferred from measurements of photosynthesis in leaves of transgenic tobaco with reduced Rubisco content. Planta, 195: 33-47.

Wang, K. Y., Kellomaki, S. and K. Laitinen. 1996. Acclimation of photosynthetic parameters in Scots Pine after three years exposure to elevated temperature and CO_2. Agricultural and Forest Meteorology, 82: 195-217.

Weis, E. 1981. Reversible heat-inactivation of the calvin cycle: a possible mechanism of the temperature regulation of photosynthesis. Planta, 151: 33-39.

Wullschleger, S.D. 1993. Biochemical limitation to carbon assimilation in €3 plants. A retrospective analysis of A/Ci curves from 109 species. Journal of Experimental Botany, 44: 907-920.